

## DIEL VERTICAL MIGRATION AND PHOTORESPONSES OF THE CHAETOGNATH *SAGITTA HISPIDA* CONANT

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### ABSTRACT

In estuarine waters at Beaufort, North Carolina, adult *Sagitta hispida* perform a diel vertical migration. By day, few adult chaetognaths are found in the 7 m water column. Shortly after sunset their numbers increase rapidly at all depths. We hypothesized that the evening ascent is dependent on photoresponses elicited by some aspect of the change in light intensity occurring at sunset. In the laboratory, *S. hispida*'s upswimming increases markedly whenever light intensity drops below  $10^{16.7}$  photons  $m^{-2} \cdot s^{-1}$ . Animals adapted to light intensities below this level, and to darkness, show strong upswimming. This indicates that continuously decreasing light intensity is not required to maintain the upswimming response. In the field, in the afternoon and evening, downward irradiance values of  $10^{16.7}$  photons  $m^{-2} \cdot s^{-1}$  are found only at sunset. These findings suggest that the daily ascent of *S. hispida* occurs as an all-or-none phenomenon, dependent only on exposure to light intensities below approximately  $10^{16.7}$  photons  $m^{-2} \cdot s^{-1}$ . This threshold intensity for ascent lies above the threshold for photoreception in this species, suggesting that the ascent begins as a positive phototaxis. However, experiments in which light direction was reversed indicated that the ascent is geotactic or photokinetic, since changes in light direction had little bearing on the orientation of the upswimming response.

### INTRODUCTION

In surveys of the vertical distribution of zooplankton, chaetognaths are often found to perform a diel vertical migration (Alvarino, 1965). This type of migration is characterized by a twilight or nighttime ascent to shallow levels and daytime descent to greater depths (Hutchinson, 1957). For all zooplankton, light is considered the most important environmental factor involved in the control of diel vertical migration (Forward, 1976).

Partly on the basis of observations on chaetognaths, Michael (1911) and later Russell (1927) proposed that diel vertical migration results as zooplankton move up or down in an effort to maintain their position in some optimal or preferred range of light intensities. Support for this proposal (the preferendum hypothesis) came from studies of the movement of the oceanic deep scattering layer, which sometimes remains within a particular narrow range of light intensities during a diel vertical migration (Boden and Kampa, 1967). More recently, Forward *et al.* (1984) have shown that vertically migrating estuarine crab larvae aggregate during daytime near the depth where the irradiance corresponds to their threshold intensity for phototaxis. During

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sunset, the larvae ascend as this particular irradiance value (isolume) is found higher in the water column.

An alternative hypothesis relating vertical migration and photobehavior was proposed by Clarke (1933) and Ringelberg (1964). They suggested that the initiation of vertical migration depends on the rate and direction of change in light intensity at sunset and sunrise. Evidence in support of this hypothesis came from studies of the photoresponses of the cladoceran *Daphnia*, which accelerates its upswimming movements as a function of the rate of decrease in light intensity (Ringelberg, 1964). A similar relationship holds between *Daphnia*'s downswimming and the rate of increase in light intensity (Daan and Ringelberg, 1969). In addition, Buchanan and Haney (1980) observed that vertical migrations of arctic zooplankton are dependent on the rate of change of light intensity.

Recently, Stearns and Forward (1984) studied the photobehaviors responsible for the vertical migration of the copepod *Acartia tonsa*. Light can act to control, initiate, and/or direct vertical migration (Bainbridge, 1961). For *A. tonsa*, photoresponsiveness is controlled by the level of light adaptation. The initiating cues for vertical movement are the direction and rate of change in light intensity. Light is not used as a directional cue for vertical movements.

The work reported here was undertaken to examine the role of photobehavior in the diel vertical migration of the chaetognath *Sagitta hispida* Conant. Details of the timing of the ascent phase of the migration were determined in field studies. To determine how light might control, initiate, or direct the migratory ascent, the field observations were compared to experimentally elicited photoresponses involving upswimming. The results suggest that *S. hispida*'s vertical migration conforms to the preferendum hypothesis, and light acts only to control vertical movement.

## MATERIALS AND METHODS

### *Field studies*

Chaetognaths were collected from a platform attached to the Piver's Island Bridge at Beaufort, North Carolina. Total depth at this location ranged from 5 to 7 m, depending on the state of the tide. Stratified plankton samples were obtained by suspending opening/closing nets in the tidal flow beneath the bridge at 1, 3, and 6–7 m. Net mouth diameter was 0.5 m, and each net was equipped with a calibrated flowmeter (TSK, Yokohama). The nets were made of 0.5 mm mesh Nytex<sup>®</sup>, and retained animals >6 mm in length. These chaetognaths were of Stage II or III of Russell's (1932) sexual maturation classification scheme (maturing male and female gonads).

For two field studies, sets of stratified plankton collections were made at intervals of approximately 3 h over the course of two to three days. On three other occasions, 5–7 collections were made at intervals of about 40 minutes immediately prior to and after sunset. Samples were preserved in borate-buffered 5% formalin in sea water.

During each field study, water samples were collected at 1, 3, and 6–7 m, and their temperatures and salinities measured using, respectively, a thermometer and refractometer (American Optical). During the two longer field studies, these measurements accompanied each series of plankton samples. During the short term field studies, temperature and salinity were measured at the beginning, midpoint, and end of each study.

During two of the short-term studies, field light intensity was measured with a submersible radiometer (Kahl, model 268 WA 310). This device was fitted with a

cosine collector, and measured downwelling irradiance. The spectral response of the radiometer was restricted to the region 400–620 nm through insertion of a filter (Corning 4-72). *Sagitta hispida* is most sensitive to light in this region of the visible spectrum, with maximum sensitivity at 500 nm (Sweatt and Forward, 1985). The radiometer was calibrated with a laboratory photometer (EG & G model 550), and the field measurements expressed as photons  $\text{m}^{-2} \cdot \text{s}^{-1}$ . On the evening before the field study of 17 September 1982, light intensity was measured at several depths during sunset in order to document the rates of change in light intensity at the depths where the plankton were to be sampled. During subsequent field studies, irradiance was measured only at the surface, and the values at depth determined through calculations based on the previously determined light profile.

### *Photobehavior experiments*

For experimental studies, *Sagitta hispida* were obtained from the field study site at night, when the animals were most abundant in the water column. Conditions of capture and maintenance of the chaetognaths are described by Sweatt and Forward (1985). Sweatt (1983) found no evidence that *S. hispida*'s vertical migration is controlled by endogenous rhythms in activity or phototaxis. Hence the experiments reported here were designed to assess the tendency of chaetognaths to swim upward following a decrease in light intensity within the range of intensities found in the field near sunset. *S. hispida* is negatively buoyant, and its swimming pattern consists of repetitive head-upwards darting motions, each followed by a period of passive descent. In prolonged darkness and under prolonged overhead light (fluorescent room lights), this behavior causes most of the animals to stay near the top of a vessel. Therefore, to be able to observe unequivocal upswimming responses following changes in light intensity, chaetognaths were initially confined near the bottom of a vessel, and released after light intensity was manipulated. The procedure is described in detail below.

Experiments were performed only with animals which had been light adapted for at least 1.5 h prior to testing. Light sources for adaptation and stimulus presentation were slide projectors, equipped as described by Sweatt and Forward (1985). Light adaptation wavelength was 500 nm, obtained with an interference filter (Ditric Optics; half band width 9 nm). Using a mirror, the adaptation light was directed downward onto the chaetognaths, which were held in groups of 13–15 in 50 ml beakers. Before every experiment, light intensities were measured with a laboratory photometer (EG & G Model 550). The photometer probe was placed on the optical axis of the projector-mirror apparatus, at the level of the beakers, and directly faced the light source.

For experimentation, the projector used to present the test stimulus was equipped with a Corning 4-94 glass filter. This filter provided a near natural spectral distribution for the chaetognaths, in that its maximum photon transmission occurs at 560 nm (half band width 80 nm). This wavelength is close to the spectral transmission maximum for water in the Beaufort area (Sweatt, 1983). The stimulus light beam was collimated with several lenses set on an optical bench, and reflected downward onto the test vessel using a large mirror. All optical components except the mirror were situated behind a light-tight partition, out of view of the test vessel.

The test vessel was a transparent Lucite® chamber divided along its vertical axis into five equivalent sections by a set of removable partitions. The partitions were attached to a handle and could be moved in unison (see Fig. 1). With the partitions withdrawn, the portion of the vessel accessible to the animals was 30 cm high, with

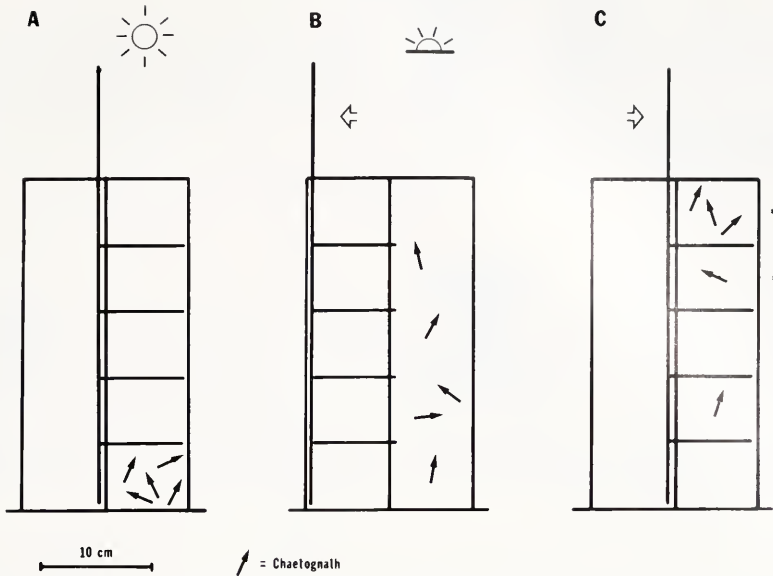


FIGURE 1. Diagram of experimental procedure for tests of upswimming by *S. hispida*. A. At original adaptation intensity, animals are placed at bottom of chamber, and partitions slid into place. B. Light intensity is manipulated, and, fifteen minutes later, the partitions are withdrawn. C. Three minutes later, partitions are replaced. Those animals found in uppermost two sections of the vessel are considered the percent upswimming.

a cross section  $3 \times 5$  cm. Light intensities were measured as described above except that the probe was placed immediately below the empty chamber.

The basic procedure for the experiments is described here. Details concerning light intensities used in the experiments are given with the results. In performing a test, 13–15 light adapted adult *S. hispida* were pipetted to the bottom section of the test vessel and the partitions were slid into place. The vessel was then filled with filtered sea water and placed in the stimulus beam, the intensity of which was adjusted to match the original adaptation intensity. Following a one minute pause to allow the animals to recover from the transfer to the test vessel, the intensity of the stimulus beam was reduced by placing a neutral density filter in the light path, or the light source was switched off. In a third test condition, light intensity was not changed from the original adaptation intensity. After a fifteen-minute waiting period at the new light intensity, or in darkness, or at the original adaptation intensity, the partitions of the test vessel were removed in a smooth, gentle motion. Three minutes later, the vertical distribution of the animals was determined (Fig. 1). The proportion of animals swimming in the two uppermost sections of the vessel was recorded as the percent upswimming. The three-minute response period was chosen on the basis of preliminary experiments in which initial upswimming responses tended to be completed within three minutes. For one set of experiments, the configuration of the light source, mirror, and test vessel was altered so that the stimulus was presented from below the animals.

The fifteen-minute waiting period was chosen to ensure that all startle responses were extinguished by the time the partitions were removed. Under highly directional illumination, *S. hispida* swims very quickly toward the light source in reaction to



mechanical shock or sudden reductions in light intensity. This reaction was first described for *Sagitta crassa* by Goto and Yoshida (1981), who called it target-aiming behavior. It is unlikely that this transient response is related to vertical migration, and it was avoided by pausing between light intensity reduction and withdrawal of the chamber partitions.

## RESULTS

### Field studies

The field studies were planned to control for the possibility that migration is related to tidal phase. Some estuarine zooplankton show a tidal vertical migration pattern (e.g., decapod larvae; Cronin, 1982). Thus in the August 1981 study, the time near sunset (when the animals would likely be migrating) coincided with a rising tide. In the June 1982 study, a falling tide occurred near sunset. During each study temperatures generally fell at night and rose during the day (Fig. 2). The variation in salinity followed the tidal cycle, with lowest salinities occurring at low tide, and highest salinities at high tide (Fig. 2).

Changes in *Sagitta hispida* abundance are shown in Figure 3. Temporal trends in abundance variations were compared between depths by calculating Spearman's rank correlation coefficient (Snedecor and Cochran, 1967). Results showed that there were coherent trends in abundance changes at the three sampling depths in 1981 (correlation coefficients  $\leq 0.850$ ,  $P < .05$ ). In the 1982 study (Fig. 3B), while a general increase in abundance in the water column at night was evident, there were no strongly correlated or statistically significant temporal trends across depth (correlation coef-

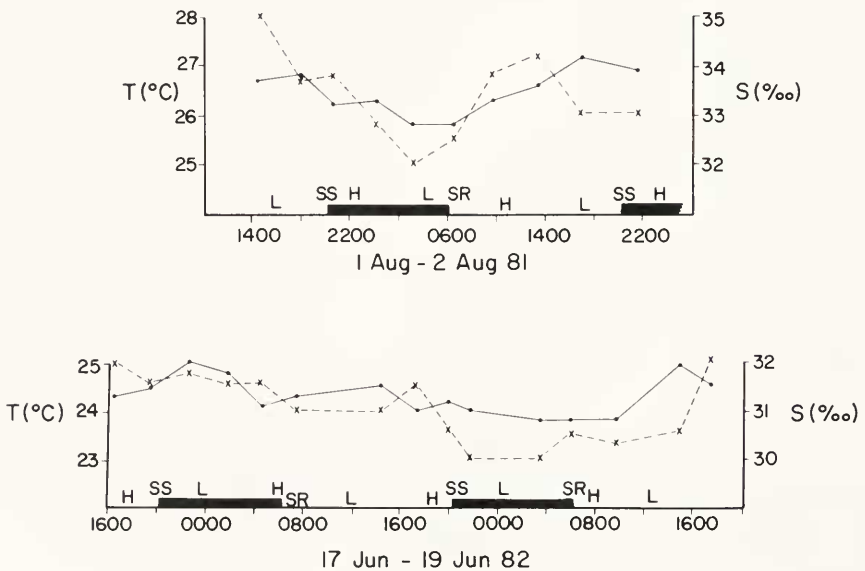


FIGURE 2. Temperature (solid line) and salinity (dashed line) at Piver's Island Bridge, Beaufort, NC, during the studies of diel vertical migration. Values plotted are means of measurements taken at 1, 3, and 6-7 m. There was little variation with depth:  $T: \pm 0.2^\circ\text{C}$ ;  $S: \pm 0.4$  ppt. Dark horizontal bar indicates period between sunset (ss) and sunrise (sr). H = high tide; L = low tide.

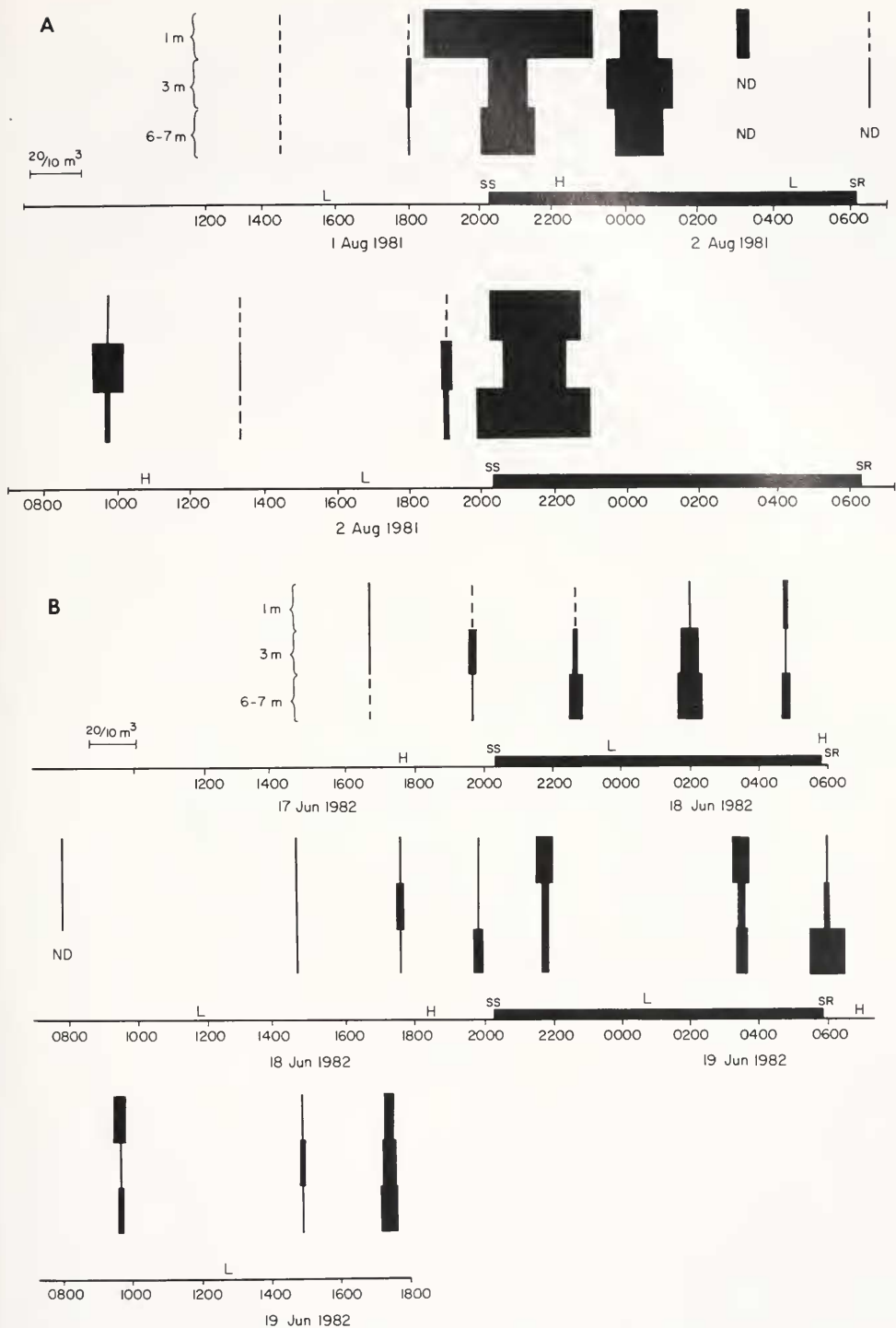


FIGURE 3. Vertical distribution of *Sagitta hispida* at Piver's Island Bridge, Beaufort, NC. A. 1-2 August 1981. B. 17-19 June 1982. For each sampling time, abundance (no./10 m<sup>3</sup>) at 1, 3, and 6-7 m is indicated by rectangles with widths proportional to abundance. Solid vertical lines show abundances < 1/10 m<sup>3</sup>. Dashed vertical lines show abundance = 0. ND = no data. Other symbols as in Figure 2.

ficients  $\leq 0.510$ ). This result may have been due to the fact that, in June 1982, *S. hispida* abundance was generally very low.

The three short-term field studies were also planned so that the chaetognaths were sampled at sunset on both rising and falling tides (Fig. 4). As before, temperature and salinity varied little with depth. Temperatures generally fell after sunset, and salinities rose or fell in correspondence with the phase of the tide. During each study, *S. hispida* abundance increased dramatically at each sampling depth shortly after sunset (Fig. 4).

The daily variations in the abundance of *S. hispida* in the water column indicate that this species performs a vertical migration, and ascends in the evening during both rising and falling tides (Fig. 3). The increase in near-surface abundance at night

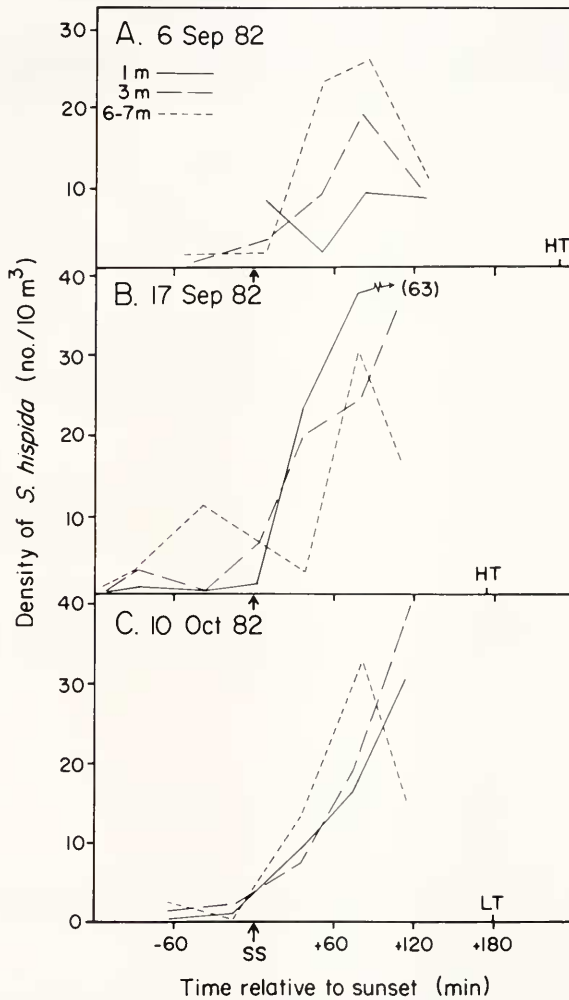


FIGURE 4. Abundance of *Sagitta hispida* at Piver's Island Bridge, Beaufort, NC, during three short term field studies. Values are plotted separately for each sampling depth. ss = time of sunset. HT, LT = times of high and low tide.

is particularly striking in the study of August 1981 (Fig. 3A), and in the short term investigations (Fig. 4).

Figure 5A shows the downward irradiance at several depths during sunset at the study site on the day before the second short term field study (Fig. 4B). Figure 5B shows surface irradiances and extrapolated bottom irradiances at the time of the second and third field studies (Fig. 4B, C). Surface irradiance differs between dates due to variations in cloud cover. On each date, downward irradiance was relatively constant during the late afternoon, and fell nearly simultaneously at all depths during

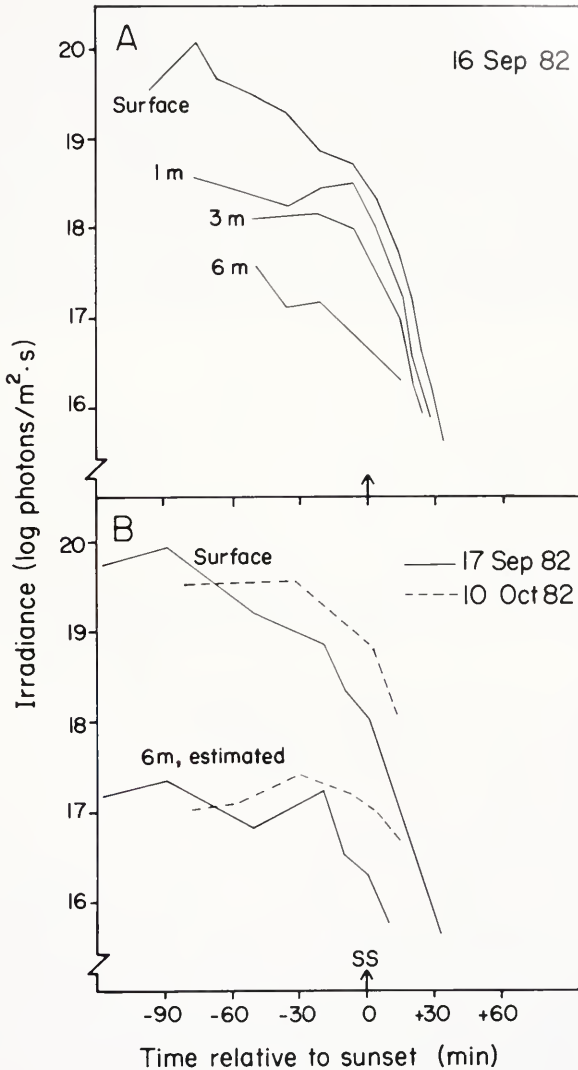


FIGURE 5. Downward irradiance at Piver's Island Bridge, Beaufort, NC. A. Irradiance measured at several depths during sunset, 16 September 1982. B. Irradiance measured at the surface during two of the field studies: 17 September and 10 October 1982. Values plotted for 6–7 m for these data were extrapolated from surface measurements.



sunset. The most rapid decreases in irradiance occurred just after sunset. At sunset, irradiance values over the 7 m water column ranged from  $10^{16}$  to  $10^{19}$  photons  $m^{-2} \cdot s^{-1}$ .

### Photobehavior experiments

In the first series of experiments, upswimming was tested for animals adapted to each of five different light intensities (Fig. 6). Animals were used only once in any experiment. Upswimming was tested at each of the original adaptation intensities (LA), at one log unit below those intensities ( $LA^{-1}$ ), and in darkness (D). Statistical comparisons were made between responses measured under the three test conditions at each adaptation intensity (one-way analysis of variance). In one case, tests were conducted only at the original adaptation intensity and in darkness. In the five sets of tests, upswimming responses were weakest when measured at the original adaptation intensity. Leaving animals in darkness invariably led to a stronger response. Reducing the light intensity to one log unit below the original adaptation intensity had variable effects. At the two highest original adaptation intensities, upswimming following such intensity reductions ( $LA^{-1}$ ) was not significantly different from the response observed with no change in light intensity (LA). However, at two lower adaptation intensities, responses following the one log unit reduction became more like those measured for animals left in darkness (D). This indicates that reducing the intensity by one log unit ( $LA^{-1}$ ) led to marked and significant increases in upswimming (relative to the

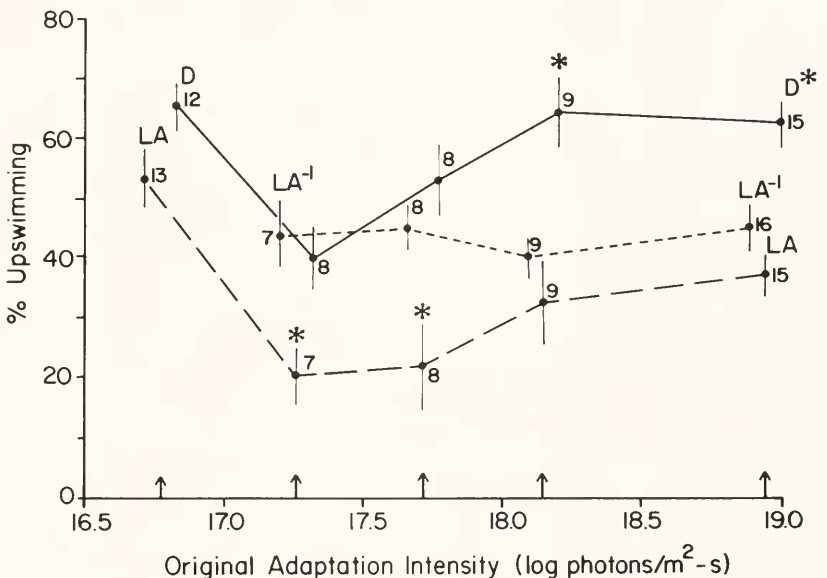


FIGURE 6. Upswimming responses of *Sagitta hispida* adapted to various light intensities. Means and standard errors are shown on the vertical axis. Sample size for each experimental condition is indicated next to mean response level. Ordinate indicates original adaptation intensity. For each set of tests, animals were adapted to the original light intensity for at least 1.5 h prior to being tested under one of three conditions: LA = upswimming measured 15 minutes after animals were placed in test chamber at the original adaptation intensity;  $LA^{-1}$  = after 15 minutes in test chamber at an intensity 1 log unit lower than the original adaptation intensity; D = 15 minutes after being placed in test chamber in darkness. Separate statistical comparisons (ANOVA) were made for data obtained using animals adapted to each of the respective original adaptation intensities. \* Indicates the experimental condition for which upswimming responses were significantly different from the other two conditions ( $P < .05$ ).

LA condition) only when the final light intensity was  $10^{16.72}$  photons  $m^{-2} \cdot s^{-1}$  or lower (Fig. 6). Finally, at the lowest original adaptation intensity ( $10^{16.8}$  photons  $m^{-2} \cdot s^{-1}$ ), upswimming responses in darkness and in light (without intensity reduction) were strong and not significantly different from each other.

In the second series of experiments, upswimming was measured for animals originally adapted at  $10^{17.66}$  photons  $m^{-2} \cdot s^{-1}$ , and irradiated from above or below. Upswimming was tested at the adaptation intensity, and at one log unit below this intensity. This adaptation intensity was chosen because animals had previously shown significantly different responses at a comparable intensity and at one log unit below it (Fig. 6, adaptation intensity  $10^{17.72}$  photons  $m^{-2} \cdot s^{-1}$ ). For comparison with previous experiments, upswimming was also measured for animals kept in darkness.

Results are displayed in Figure 7. As seen in the previous experiment, upswimming increased after light intensity reduction. In darkness, the usual strong upswimming response was observed. No downswimming was observed for animals irradiated from below. The responses of irradiated animals were compared using two-way analysis of variance. Interaction between light intensity and direction was significant at  $P = .046$ . For an interaction with significance at this level, it is still useful to compare main effects. A strong main effect was observed for light intensity alone ( $P < .01$ ) while light direction alone had no significant effect on the upswimming response. Comparison of mean response levels (Bonferroni's multiple comparison) indicated that irradiation at the reduced intensity ( $LA^{-1}$ ) elicited a significantly greater mean response than irradiation at the original adaptation intensity ( $P < .05$ ).

#### DISCUSSION

The nighttime abundance of adult *Sagitta hispida*, coupled with their virtual absence during the day, provides strong evidence that this species performs a diel vertical migration. Animals larger than 6 mm are nearly absent from daytime samples, while their abundance increases markedly at all depths after sunset (Figs. 3, 4). The abundance fluctuations correlate with day-night cycles, and the evening ascent occurs on both rising and falling tides. Figures 2 and 3 show that in the hour after sunset, temperature and salinity change little, while the abundance of *S. hispida* rises sharply. Thus, the post-sunset elevation of chaetognath abundance in the water column is not necessarily associated with movement of a distinct new water mass (with new plankton organisms) into the sampling area.

The short term studies provided further evidence for the close association of sunset with the daily appearance of large numbers of *S. hispida* in the water column (Fig. 4). Migration was again observed on both rising and falling tides. Based on the data collected on 17 September 1982 (Fig. 4B), the upward migration begins no earlier than 10 minutes after sunset (beginning of increases in animals at 3 m). By this time, irradiance near the bottom of the estuary would have fallen below the daytime level of approximately  $10^{17}$  photons  $m^{-2} \cdot s^{-1}$  (Fig. 5).

The most striking aspect of the migration of the larger *S. hispida* is their almost total absence from the water column during the day. Since plankton samples were collected to within 0.5 m of the bottom, and few chaetognaths were found in any daytime samples, it appears that these animals stay very close to the bottom during daylight. Similar observations have been made for *Sagitta elegans*, another chaetognath found in coastal waters (Pearre, 1973; Weinstein, 1973; Sweatt, 1980).

*S. hispida* can attach itself securely to the sides of glass and plastic aquaria (Reeve and Walter, 1972). This species also tolerates prolonged contact with natural substrates, such as sand (pers. obs., A.J.S.). Considering these observations and the vertical distribution data, it seems possible that older *S. hispida* could maintain contact with the bottom of the estuary during the daytime, even in the presence of tidal currents.

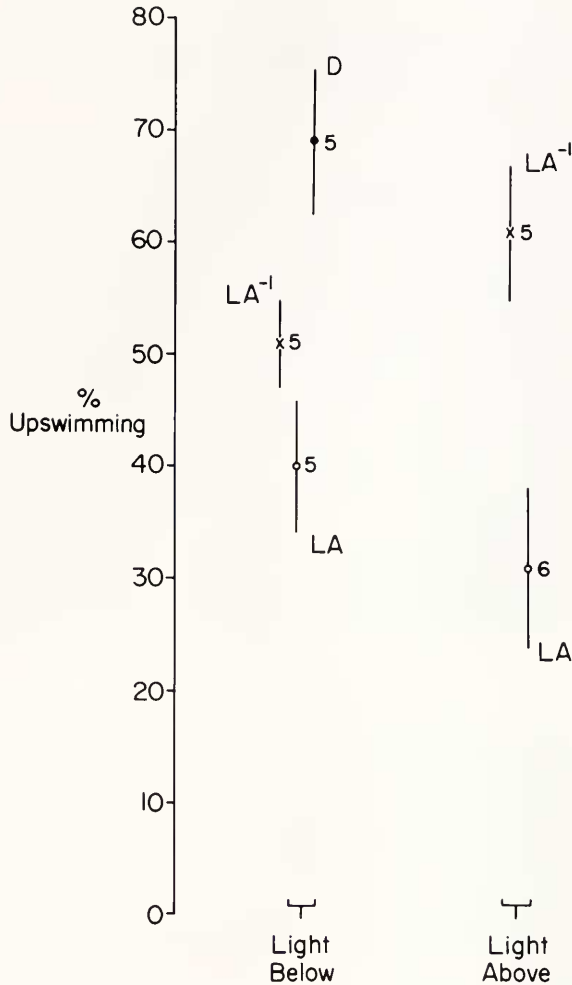


FIGURE 7. Upswimming by *Sagitta hispida* with reversal of light stimulus direction. Means, standard errors, and sample sizes are shown as in Figure 6. Original adaptation intensity was  $10^{17.66}$  photons  $m^{-2} \cdot s^{-1}$  for all tests (see text for rationale). Arbitrary ordinate indicates whether animals were irradiated from above or from below. Other symbols as in Figure 6.

Based on the sampling methods used (horizontal plankton tows) one cannot say whether the continued nighttime appearance of *S. hispida* results from sustained upswimming by individual animals or from rapid fluxes of animals between all depths (Pearre, 1979). Therefore, the behavior which initiates the post-sunset upward movement of *S. hispida* is the only migration-related behavior the direction and timing of which are known with certainty. We hypothesized that this behavior is dependent on photoreception for its initiation.

Light can act to control, initiate, and direct vertical movements of zooplankton (Bainbridge, 1961). Studies have shown that light adaptation level controls responsiveness of zooplankton for migration (Stearns and Forward, 1984), while the actual cue which initiates vertical movement can be a change in light intensity (Ringelberg, 1964; Daan and Ringelberg, 1969; Stearns and Forward, 1984). In addition, overhead

light can act as a directional cue for orienting the animal for swimming upward or downward.

The results of the photobehavior experiments show that reductions of light intensity are followed by increased upswimming by adult *S. hispidus*. Reduction of the light intensity by one log unit elicited enhanced upswimming when the final stimulus intensity was  $10^{16.72}$  photons  $m^{-2} \cdot s^{-1}$  or lower. It is important to note that upswimming was not enhanced following one-log unit reductions which ended at intensities above this level (Fig. 6). For all adaptation intensities, relatively strong upswimming was observed following a decrease in intensity to zero (darkness).

These results support the hypothesis that the ascent phase of the vertical migration of *S. hispidus* involves visual behavior. The type of upswimming response observed following experimental reductions in light intensity could well account for the post-sunset ascent of these animals. In addition, it appears that sustained upswimming by *S. hispidus* does not depend on continuously changing light intensity or on particular rates of change of intensity. This is evident from the experimental results, where upswimming was enhanced even 15 minutes after the light intensity was reduced. Even more salient was the observation of strong upswimming by animals exposed to a constant low light intensity. The lack of a requirement for continuously changing light levels for initiation of ascent was evident in the field data, where the concentration of *S. hispidus* in the water column continues to increase even two hours after sunset (Fig. 4). By this time light intensity at the surface would have reached a constant low value.

At Piver's Island Bridge, adult *S. hispidus* appear to spend the day near the bottom, or at 6–7 m depth. At this depth, light intensities below  $10^{16.72}$  photons  $m^{-2} \cdot s^{-1}$  are reached only at sunset and sunrise (Fig. 5). Based on these field observations and the experimental findings, we proposed that the ascent phase of the vertical migration of *S. hispidus* is controlled by light intensity, and occurs once the intensity falls below a particular level in the evening. This "threshold" light intensity appears to lie near  $10^{16.7}$  photons  $m^{-2} \cdot s^{-1}$ .

The concept of a threshold for ascent is a variation of the preferendum hypothesis (Michael, 1911; Russell, 1927). It could be predicted that, without depth restrictions, the center of distribution for a population of adult *S. hispidus* should lie near the depth corresponding to the threshold intensity of  $10^{16.7}$  photons  $m^{-2} \cdot s^{-1}$ . Animals finding themselves much below this depth would tend to ascend, once they were adapted to subthreshold intensity. Those at shallower levels would experience net sinking due to a reduced frequency of upswimming movements upon adaptation to suprathreshold intensities. This prediction should be tested through field studies in deep water.

The threshold effect described for *S. hispidus* is seen in several other animals which exhibit daily behavioral cycles. Dreisig (1980) reported a threshold effect for nocturnally active moths. The beginning of evening flight activity in these animals coincides with the onset of particular low levels of illumination, and is not initiated by the rate of change in light intensity (Dreisig, 1980).

Another example of a threshold effect for evening activity has been shown by Forward *et al.* (1984) for vertically migrating larvae of the crab *Rhithropanopeus harrisi*. Over the course of the day, larvae in the field appear to congregate at depths where the intensity is close to the lower threshold for phototaxis in these animals. Forward *et al.* (1984) also showed that, at suprathreshold intensities, *R. harrisi* larvae sink, while at subthreshold intensities or in darkness, the animals display a negative geotaxis (upswimming).

For the crab larvae, the threshold for ascent coincides with the threshold for phototaxis, or, as determined by Forward *et al.* (1984), the threshold for vision. The



crab larvae may shuttle between depths of perceived light and perceived darkness as they rise and sink near the depth corresponding to their visual threshold. For *S. hispidus*, however, the threshold light intensity for ascent is well above the threshold for dark adapted phototaxis (ascent threshold:  $10^{16.7}$  photons  $m^{-2} \cdot s^{-1}$ ; phototaxis threshold: near  $10^{13.0}$  photons  $m^{-2} \cdot s^{-1}$ ; Sweatt and Forward, 1985). It may be that perception of each threshold is mediated by a different component of the chaetognath visual system. By analogy with the duplex retina of some vertebrates, *S. hispidus* may possess photoreceptors specialized for vision at different light intensities. Morphological evidence for heterogeneity of photoreceptors in *S. hispidus* is presented elsewhere (Sweatt, 1983).

The second set of experiments was designed to test the hypothesis that light direction affects the swimming orientation of *S. hispidus* at intensities below the threshold for ascent. Since *S. hispidus* can perceive light intensities below the threshold for ascent, it may use light as a directional cue during the evening ascent. Thus the ascent might result from positive phototaxis. Alternatively, light direction may be irrelevant to swimming orientation during the ascent. In this case, the ascent could result from negative geotaxis and/or increased activity (photokinesis). Since *S. hispidus*'s normal swimming mode includes active upward movement (followed by passive descent), no attempt was made to experimentally distinguish between geotaxis and photokinesis. However, since *S. hispidus* can attach to surfaces, such as the bottom of the estuary, it is conceivable that the evening ascent could initially involve arousal of animals from immobility. This would be a purely photokinetic effect.

In the relevant experiment, animals were irradiated from above or from below at intensities both greater than and less than the threshold intensity for ascent. Analysis of the results indicated that light intensity and direction may act together to influence the upswimming response, though their statistical interaction is not particularly strong. Ignoring this possible interaction, it was found that light intensity alone has a much greater influence on upswimming than does light direction alone. These results are interpreted to mean that *S. hispidus*'s upswimming response at low light intensities is basically a photokinesis or negative geotaxis, and that a directional light response (phototaxis) is not deeply involved in this behavior. Light intensity apparently serves only to modify the magnitude of the upswimming response, since no downswimming was observed. A similar scheme of light-controlled geotaxis was invoked by Esterly (1919) and Pearre (1973) to explain the migratory ascent of other chaetognaths.

Further evidence against the primary involvement of phototaxis is that *S. hispidus*'s migratory ascent continues into the night in constant light intensities which lie below the visual threshold (Figs. 3, 4). This is consistent with the experimental observation that *S. hispidus* swims upward in darkness. Such behavior was also reported for other chaetognaths by Esterly (1919), Pearre (1973), and Goto and Yoshida (1981). This aspect of chaetognath swimming behavior can only result from orientation with respect to gravity. A likely candidate for gravity perception may be the mechanoreceptive ability of chaetognaths. These animals possess vibration-sensitive hair fans, or setae, distributed over the surface of the body (Feigenbaum, 1978). The hair fans function in prey detection (Feigenbaum and Reeve, 1977), but may also play a part in orienting the body in space. During the sinking phase of *S. hispidus*'s characteristic dart and sink swimming pattern, the mechanoreceptors may be stimulated by the shear field around the animal. This recurrent, predictable stimulus could provide an animal with information as to which way is up, even in the absence of light. Strickler (1982) recently speculated that copepods take advantage of a similar set of circumstances, including a stereotypical swimming pattern and mechanoreception, to determine the direction upward.



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